Reproduction and feeding of Sagitta enflata in the Humboldt Current system off Chile

Ricardo Giesecke and Humberto E. González


This study is based on 3 years (August 2002 – July 2005) of monthly zooplankton sampling at a fixed station located 18 km off Coliumo Bay (36°S), Chile. The reproduction of Sagitta enflata, its feeding rate, specific daily ration, and prey selectivity were analysed and related to several environmental variables: temperature, salinity, dissolved oxygen, chlorophyll a concentrations, and both meso- and microzooplankton abundance. The main predatory activity of S. enflata was centred on the copepods Paracalanus parvus, Oithona spp., and Calanus chilensis. These three species were consumed at different rates, depending mainly on the maturity of the S. enflata population. When Stages I and II individuals dominated, predation focused on the small P. parvus and Oithona spp., whereas more mature populations (Stages III and IV) preyed selectively on C. chilensis. The mean specific daily ration of 0.1 d^{-1} increased to 0.5 d^{-1} before and during maturation. The reproductive phase of S. enflata was closely coupled with the abundance of nauplii, suggesting that chaetognath reproduction paralleled that of copepods, most likely to diminish the mortality of its offspring resulting from starvation. The relationships between these were included in a conceptual model and their ecological significance is discussed.

Keywords: chaetognaths, Humboldt Current system, reproduction, Sagitta enflata.

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R. Giesecke: Centre for Oceanographic Research in the Eastern South Pacific (COPAS), Concepción, Chile, and Graduate Programme in Oceanography, Departament of Oceanography, Universidad de Concepción, Concepción, Chile. H. E. González: Centre for Oceanographic Research in the Eastern South Pacific (COPAS), Concepción, Chile, and Institute of Marine Biology "Jürgen Winter", Universidad Austral de Chile, Valdivia, Chile. Correspondence to R. Giesecke: tel: +56 63 22 1559; fax: +56 63 22 1455; e-mail: cgiesecke@udec.cl.

Introduction

Many studies demonstrate that fecundity and development in chaetognaths are functions of temperature (Sameoto, 1971; Conway and Williams, 1986). Therefore, latitude may be a major factor in determining the number of generations produced in an annual cycle (Ghirardelli, 1968). In general, the number of generations increases as the distance from the poles becomes greater (Owre, 1960). The association between these two variables can only exist under conditions in which food resources—both in terms of quality and quantity—are not limiting. Poor food quality or quantity would lead to a low or negative growth rate (Reeve, 1970) as a result of the lack of carbon or nitrogen resources available for sustaining the metabolic demands of growth and reproduction (e.g. the starvation of mature Sagitta hispida results in a cessation of reproductive activity and weight loss; Reeve and Cosper, 1975). Despite a significant effort to determine the reproductive pulses of chaetognaths (Alvarino, 1965), no attempt has been made to explain the processes favouring reproduction. The latter is crucially important because it could also explain the interannual discrepancies in periodicity and duration of the chaetognath breeding and life cycles observed in several studies (McLaren, 1966, 1969; Khan and Williamson, 1970; Conway and Williams, 1986; Sameoto, 1987). There is some evidence that reproduction of chaetognaths may be linked to the increase of copepod abundance during spring and summer (Zo, 1973; King, 1979; Ohman, 1986), suggesting a dependence on prey for reproduction.

The processes involved in chaetognath maturation and breeding are key to understanding their population dynamics; such information may allow some predictability of chaetognath populations. The goal of this paper is to identify and evaluate the abiotic (temperature, salinity, dissolved oxygen concentrations) and biotic (prey availability, feeding behaviour) variables responsible for the maturation of chaetognaths in the central Humboldt Current system (HCS). Sagitta enflata was selected for this purpose. It is the dominant species in the HCS and one of the most abundant and widely distributed epipelagic chaetognath species in the world oceans (Alvarino, 1965). The study was conducted in the HCS, a major eastern boundary current system with one of the highest primary production rates measured for coastal environments (4–20 g C m^{-2} d^{-1}; Daneri et al., 2000) and high seasonal heterogeneity. The biological productivity of this system is mainly supported by the intrusion of high-nutrient and oxygen-depleted equatorial subsurface water (ESSW) during austral spring and summer when northerly winds prevail. During austral autumn and winter, increased river run-off and decreased upwelling periodicity promote a system dominated by small diatoms and net heterotrophy. These characteristics make this system especially interesting for studying biological associations and dynamics that are coupled
to large-scale responses such as the El Niño Southern Oscillation and the Pacific Decadal Oscillation, and can provide some insight into possible responses to ongoing climate change.

Material and methods
Oceanographic properties
The study was conducted at Station 18 (St. 18) off Coliumo Bay (36°30'S 73°07'W; Figure 1). Sampling was conducted approximately monthly between August 2002 and July 2005. Samples were taken twice a month during favourable weather (September 2002 to April 2004) and partially halted at the end of austral summer and beginning of winter owing to unfavourable weather. For each sample, water temperature, conductivity, and dissolved oxygen profiles were obtained with a CTD-O (SeaBird SBE 19 Plus). Variables such as temperature, salinity, and dissolved oxygen concentrations were analysed as mean values of the integrated water column (0–80 m). Upwelling events were identified using the Bakun upwelling index (Bakun, 1978). Wind data (velocity, direction), recorded four times a day every 6 h (from 02:00 to 20:00), were obtained from the weather station at Carriel Sur airport. The mean daily zonal wind intensity (m s⁻¹) was used to calculate the daily mean wind drag coefficient and windstress according to Wu (1982). The mean daily Ekman offshore transport (Bakun upwelling index, \( M_u \)) was calculated for the 100 m coastal line as:

\[
M_u = \left( \frac{\tau^*}{\rho f} \right) \times 100,
\]

where \( \tau^* \) is windstress, \( \rho \) the water density, and \( f \) the Coriolis parameter.

The Bakun upwelling index was calculated for each sampling date using 5 d of mean daily water transport (m³ s⁻¹) data before the sampling date. Only positive upwelling events that exceeded 10 m³ s⁻¹ were considered (Parada et al., 2001).

Zooplankton collection and analysis
Zooplankton samples were collected using a Tucker trawl zooplankton net (200 μm mesh size; 1 m² mouth area); a WP2 (once) or a Hensen net (six times) was used when the Tucker net malfunctioned. All the samples were collected during the day so that feeding patterns would not be biased by differential day and night feeding preferences. In all, 38 integrated oblique net tows were done from the bottom to the surface (ca. 0–80 m), and the volume filtered was quantified using a calibrated digital flowmeter. Zooplankton samples were fixed almost immediately in 10% tetraborate buffered formaldehyde-seawater to minimize the loss of prey in the chaetognath guts as a result of regurgitation or defaecation (Baier and Purcell, 1997). The fixed samples were analysed to estimate copepod and chaetognath abundance; the whole sample was usually analysed although, in some cases, subsamples were taken with a Folsom splitter. Sagitta enflata were sorted from the samples, measured (head to tail, excluding the caudal fin) to the nearest 0.2 mm, and the development stage identified based on Alvarinío’s (1967) classification (Table 1). The proportion of S. enflata containing prey (FCR) and number of prey per S. enflata (NPC) were also noted (Feigenbaum and González, 1984). Gut contents of S. enflata were assessed by dissection under a stereomicroscope and were further analysed under an inverted microscope (× 400 magnification) following the methodology of Øresland (1987). In almost all cases (ca. 90%), food remains were unrecognizable; the hard parts of copepod prey were identified using the mandible blades (Giesecke and González, 2004a). Appendicularians and chaetognaths in gut contents were recognized by faecal pellets and grasping spines, respectively. Copepod prey sizes were estimated from the relationship between mandible width (MW) and prosome length (PL), as used by Giesecke and González (2004a). On some occasions, large, unidentified mandible blades were found in chaetognath guts; these were later identified as belonging to Calanus chilensis. The relationship between MW and PL of this species was determined to estimate the length of the C. chilensis ingested by S. enflata.

The feeding rate on total and individual prey by species item was calculated from the equation proposed by Bajkov (1935):

\[
FR = \frac{\text{NPC} \times 24}{DT},
\]

where the daily feeding rate, or the mean number of prey ingested per 24 h (FR), is calculated from the mean number of prey ingested per chaetognath (NPC) and the digestion time (DT) in hours.

Table 1. Maturity stage classification of S. enflata according to Alvarinío (1967).

<table>
<thead>
<tr>
<th>Male gonads</th>
<th>Female gonads</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I</td>
<td>Ovaries reaching quarter or half the length of the posterior fins along the trunk</td>
</tr>
<tr>
<td>Stage II</td>
<td>Ovaries reaching to about mid-length of the extent of posterior fins on the trunk or near the anterior end of the posterior fins</td>
</tr>
<tr>
<td>Stage III</td>
<td>Ovaries nearly reaching the anterior end of the posterior fins or the posterior end of the anterior fins</td>
</tr>
<tr>
<td>Stage IV</td>
<td>Ovaries reaching the anterior end of the posterior fins</td>
</tr>
</tbody>
</table>

Figure 1. Location of time-series Station 18.
The DT of *S. enflata* was estimated from the equation proposed by Ohman (1986):

$$DT = 10.48e^{-0.086T},$$

where $T$ is water temperature (°C), estimated, in this case, as the average of the integrated water column (0–80 m) for each sampling date.

The specific daily ration (SDR) of *S. enflata* was calculated as

$$SDR_d = \frac{FR_c d}{WS_d},$$

where $FR_c d$ (µC ind.$^{-1}$ d.$^{-1}$) is the mean feeding rate in carbon weight of *S. enflata* during each sampling period ($d$), and $WS_d$ is the mean carbon weight of *S. enflata* at each sampling (µC ind.$^{-1}$). The SDR was only estimated in cases in which the number of animals with food in their guts exceeded ten individuals per sample.

The mean feeding rate in carbon weight ($FR_c d$) was estimated from

$$FR_c d = FR_n d \sum f_j W_p j,$$

where $FR_n d$ is the mean feeding rate during each sampling ($d$; prey ind.$^{-1}$ d.$^{-1}$), $f_j$ the frequency of prey ($j$) in the gut of *S. enflata* on date ($d$), and $W_p j$ the carbon weight of prey ($j$; Saito and Kierboe, 2001).

The mean carbon content per copepod prey item was estimated, based on the PL to carbon conversion proposed by Uye (1991) for *Paracalanus parvus*, Uye (1982) for *Centropages brachiatus*, Escriberno et al. (1997) for *Chileana*, Berggreen et al. (1988) for *Acartia tosa*, Sabatini and Kierboe (1994) for *Oithona spp.*, and Satapoomin (1999) for *Oncaea spp.* and *Corycaeus spp.* The mean value of the PL of each copepod species was obtained from Hidalgo and Escriberno (2007) and P. Hidalgo (pers. comm.). For large, unidentified copepods, we assumed a carbon content of 51 µg, whereas, for small unidentified copepods, we assumed a carbon content equivalent to that of a 550 µm length *P. parvus*. We used a carbon content of 5.17 µg for *Oikopleura* spp., based on the mean trunk length of 971 µm (I. Andrade, pers. comm. and a carbonlength conversion proposed by King et al. (1980).

**Dry weight and carbon content of *S. enflata***

Specimens of *S. enflata* in good condition with empty guts were isolated from natural samples according to their developmental stage, placed on preweighed GF/F filters, and dried at 60°C for 24 h to measure dry weight (DW) with a precision of ±10 µg. Carbon content was estimated according to the carbon: dry weight ratio of Batistic (2003) as

$$µgC = DW(µg) \times 0.35.$$

**Selectivity**

Selectivity of *S. enflata* for ingested prey was estimated using the Pearre’s selectivity index $C$ (Pearre, 1982). This index relies on $\chi^2$ analysis of the number of individual prey items in predator guts, compared with those available in the environment; the index was calculated as

$$C = \pm \left[\frac{(a_0 d - b_0 a_1 - n/2)^2}{a b c d e}\right]^{1/2}.$$

The terms of the equation are defined in Table 2.

The selectivity $C$ values were calculated from the relative abundance (percentage) of each zooplankton prey item ingested in relation to the total prey standing stock, where $a$ and $b$ represent the relative abundance of a particular species (A in Table 2) and all others, respectively, and subscripts $d$ and $e$ indicate the diet and the environment. The sign of the selectivity index is given by the inspection of $a_0 d - a_0 b$; the index ranges from −1 to 1. Positive values indicate selection, negative values indicate avoidance, and a value of zero indicates no selection. Statistical significance was tested with the $\chi^2$ statistic with one degree of freedom (Pearre, 1982) at a significance level of 0.05. For the analysis, we only considered sampling dates on which at least ten prey were identified in chaetognath guts.

**Maturity and reproduction**

We considered that reproduction took place when Stages III and IV were present, meaning that maximal oocyte and testis development was achieved. The percentage of Stages III and IV of the entire population was used as a reproduction index and compared with environmental variables (temperature, salinity, dissolved oxygen) through Spearman correlations. Biological variables included total prey abundance (including all prey items), chlorophyll $a$ concentration—Chl $a$ (mg m.$^{-2}$, used as a productivity proxy), unicellular microzooplankton abundance, and nauplii abundance (ind. m.$^{-3}$). The effect of feeding activity on reproduction, expressed as FCR and NPC, was also considered.

**Abundance of prey for *S. enflata* offspring**

Microzooplankton samples were collected before each zooplankton net haul at three depths (10, 30, and 80 m) using 30 l Niskin bottles. These samples were concentrated (10–30 l) by passing them through a 20 µm sieve (final volume of 100 ml). They were preserved in buffered formalin (4%) and later analysed for general taxonomic composition and abundance using an inverted microscope Olympus CK2 at ×400 (Utermöhl, 1958). As buffered formalin was used to preserve the samples, the microzooplankton may have been underestimated because of labile protozoan disintegration.

We considered that the timing of recently spawned chaetognath specimens ready to feed on microzooplankton is closely related to the maturity cycle displayed by *S. enflata*, because the age of first-feeding of *S. enflata* occurs shortly after hatching (8–9 d; Doncaster, 1902, after Pearre, 1991).

**Table 2. Terms used to calculate Pearre’s C selectivity index.**

<table>
<thead>
<tr>
<th>Species</th>
<th>A</th>
<th>Others</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diet</td>
<td>$a_0$</td>
<td>$b_0$</td>
<td>$a_0 + b_0 = d$</td>
</tr>
<tr>
<td>Environment</td>
<td>$a_e$</td>
<td>$b_e$</td>
<td>$a_e + b_e = e$</td>
</tr>
<tr>
<td>Total</td>
<td>$a_0 + a_e = a$</td>
<td>$b_0 + b_e = b$</td>
<td>$a_0 + a_e + b_0 + b_e = n$</td>
</tr>
</tbody>
</table>
Results

Oceanographic conditions

Throughout the study period, we observed a conspicuous seasonality of the physical and chemical properties of the water column (Figure 2). During austral summer and spring, the lowest mean dissolved oxygen concentrations and temperature and the highest salinity values were recorded (Figure 2b–d). These results agree with the seasonal oceanographic features, which are characterized by an intrusion of cold, oxygen-depleted, highly saline ESSW during austral spring and summer, resulting from the intensification of the northerly alongshore winds, which favour upwelling (Figure 2a).

During austral autumn and winter, we recorded the lowest salinity, resulting from the fresh-water discharge of the Bio-Bio and Itata rivers. Contrary to austral spring and summer, the oxygen-depleted waters tended to disappear from autumn to winter, and higher levels of dissolved oxygen were recorded. Sobarzo et al. (2007) published detailed information about the area’s oceanographic features.

Reproduction

During the 3 years of this study, we were able to identify at least two clear reproductive pulses that varied in magnitude and duration. A short, intense maturation process occurred from December 2002 to February 2003, with as much as 28% of the entire population reaching maturity (Figure 3a). Thereafter, the population was dominated by Stage I individuals until the onset of the next reproductive event in November 2003. Despite intense reproduction during 2002/2003, only very small numbers of smaller S. enflata (<6 mm) were captured in subsequent months (Figure 3b). The increase in smaller organisms was only noticeable after the second reproductive period, which started in mid-November 2003 and ended at the beginning of April 2004. In 2004/2005, low abundances of S. enflata (<0.29 ind. m\(^{-3}\)) did not allow an accurate interpretation of the reproductive phase. However, based on the size structure of the population in the following months, we believe a reproduction event took place during the same season (Figure 3b).

Throughout this study, Stage II specimens bearing small oocytes were almost always observed and had relative abundance patterns similar to those of the mature organisms (Figure 3a). Variables such as temperature, salinity, dissolved oxygen, and prey density had no visible effect on the maturation timing of S. enflata (Table 3); this was attributed to the extensive reproduction event observed in 2004 (ca. 5 m), which did not match the conspicuous seasonal pattern of these variables. The only variables that correlated significantly \((p < 0.01)\) with the maturity process were nauplii and microzooplankton abundance (Figure 3c; Table 3). Not only were the tendencies of both variables closely linked, but so was the magnitude of the response of each one. The increase of Chl \(a\) (Figure 3d) did not have a clear relationship with the increased nauplii abundance, which suggests winter seasons with low Chl \(a\) during which the copepod population may rely on other food resources for growth and maturity.

Feeding and prey selectivity

Copepods made up 94% of the S. enflata diet; small unidentified copepods (<700 μm PL), P. parvus, C. chilensis, and Oithona spp. made up the bulk of the ingested prey that is up to 56% of the total copepods ingested. Other species such as Corycaeus spp., A. tona, C. brachiatus, appendicularians (genus Oikopleura), and chaetognaths were ingested in smaller proportions owing to their lower in situ abundance compared with the former species. The DT of S. enflata varied between 3.5 and 4.2 h for the lowest and highest temperatures, respectively \((3.9 \pm 0.16 \text{ h, mean } \pm \text{ SD})\). The feeding rate of the main prey items (Figure 4) varied significantly during the study, with P. parvus being the most preferred prey, followed by Oithona spp. and C. chilensis. Although the general trend of S. enflata was to prey on smaller copepods (P. parvus, Oithona spp.) when Stage I individuals were dominant, the inverse pattern was observed when Stages III and IV dominated and large proportions of the larger C. chilensis were ingested.

There is a slight difference between the sizes of the chaetognaths that prey on different prey items (by size); however, because of the overlapping standard deviations, the differences are not statistically significant (Figure 5).

A more detailed look at the temporal changes in the selection patterns of the most preyed-on species (Figure 6) reveals high variability for P. parvus and Oithona spp. Both species were usually selected asynchronously, i.e. when one prey item was positively selected, the other was avoided. This occurred systematically throughout the study period. As shown in Figure 6, selectivity on both species was not related to the maturity condition of S. enflata.

![Figure 2](https://academic.oup.com/icesjms/article-abstract/65/3/361/788381/536117/788381)

Figure 2. (a) Bakun index as m\(^3\) s\(^{-1}\) over 100 m of coastline, estimated as mean value of 5 d before the sampling date. Positive values indicate offshore transport (upwelling) and negative values indicate onshore transport (downwelling); (b) Mean integrated water temperature (°C); (c) salinity; (d) dissolved oxygen (ml O\(_2\) l\(^{-1}\)) at Station 18 over the sampling period.
Calanus chilensis, on the other hand, was the only prey item that had a consistent selectivity pattern associated with \textit{S. enflata} maturity. Other prey types, particularly chaetognaths, ostracods, \textit{A. tonsa}, and \textit{C. brachiatus}, were not common in the diet and were characterized by negative or statistically non-significant selectivity values.

Although the ingestion rate was highest for the most abundant species, there was no clear correlation between the prey abundance and the number of copepod items ingested per \textit{S. enflata} (Table 4).

Neither temperature nor salinity had a strong effect on the feeding activity of this species, which was only slightly affected by low dissolved oxygen concentrations (Table 4). The effect of patchiness of chaetognaths and their prey and the possible effect of this on the interpretation of the results tended to be reduced by the use of long, oblique net tows and subsequent high filtered volumes (ca. 250 m$^2$ for Tucker nets, 19 m$^3$ for Hensen and WP2 nets).

The amount of carbon ingested by \textit{S. enflata} as a proportion of their own carbon (SDR) increased on two occasions, before and

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure3.png}
\caption{(a) Relative abundance of the maturity stages of \textit{Sagitta enflata} on each sampling date; blank spaces indicate abundances of <0.3 ind. m$^{-2}$; (b) percentage of smaller recently hatched (<6 mm) \textit{S. enflata} of the entire population; (c) mean nauplii abundance as ind. m$^{-2}$; (d) integrated chlorophyll \textit{a} (Chl \textit{a}) concentrations (mg m$^{-2}$).}
\end{figure}

**Table 3.** Spearman correlations for the maturity stages of \textit{S. enflata} with feeding activity (NPC, FCR), biological (nauplii, microzooplankton, prey abundance, chlorophyll \textit{a}), physical (Ekman offshore transport, temperature), and chemical (salinity, dissolved oxygen) variables.

<table>
<thead>
<tr>
<th></th>
<th>FCR</th>
<th>NPC (ind. m$^{-2}$)</th>
<th>Microzooplankton (ind. m$^{-2}$)</th>
<th>Prey abundance (ind. m$^{-2}$)</th>
<th>Chlorophyll \textit{a} (mg m$^{-2}$)</th>
<th>Ekman $\delta$ (m$^3$ s$^{-1}$)</th>
<th>Temperature ($^\circ$C)</th>
<th>Salinity</th>
<th>$O_2$ (ml l$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I</td>
<td>$-0.02$</td>
<td>$0.07$</td>
<td>$-0.40^*$</td>
<td>$-0.21$</td>
<td>$-0.14$</td>
<td>$-0.19$</td>
<td>$-0.12$</td>
<td>$0.07$</td>
<td>$-0.05$</td>
</tr>
<tr>
<td>Stage II</td>
<td>$-0.01$</td>
<td>$-0.12$</td>
<td>$0.36^*$</td>
<td>$0.18$</td>
<td>$0.10$</td>
<td>$0.23$</td>
<td>$0.15$</td>
<td>$-0.14$</td>
<td>$0.04$</td>
</tr>
<tr>
<td>Stages III and IV</td>
<td>$0.00$</td>
<td>$-0.08$</td>
<td>$0.56^{**}$</td>
<td>$0.47^{**}$</td>
<td>$0.08$</td>
<td>$0.19$</td>
<td>$0.16$</td>
<td>$0.14$</td>
<td>$0.20$</td>
</tr>
</tbody>
</table>

*p < 0.05; **p < 0.01.
during reproduction, ranging between 0.4 and 0.5 d⁻¹ in the most pronounced reproduction phases (2002/2003, 2003/2004; Figure 7a). During reduced or non-reproduction periods, on the other hand, the SDR was always <0.1 d⁻¹. The increase of the SDR was not a result of the ingestion of more prey per chaetognath (Figure 7b), but was caused by an increase in predation on medium-sized *C. chilensis* (Figure 4). This species is the largest food item ingested by *S. enflata*, and, therefore, accounts for a substantial fraction of the ingested carbon in the SDR. High predation rates and ingestion of multiple preys were mainly achieved by Stage I *S. enflata*, which dominated 45–60 d after reproduction (Figure 3a and b).

We tested whether the preference for feeding on *C. chilensis* during reproduction was the result of the increased size of the mature organisms or selective predation during reproduction by comparing the mean size of the organisms that preyed on *C. chilensis*. The result of this comparison revealed no significant difference (*t*-test *p* = 0.1), indicating that the selectivity is mainly related to the maturity of *S. enflata* and not a size threshold of adults during reproduction.

**Discussion**

The analysis of oceanographic and biological variables revealed a clear seasonal pattern that is triggered by the intensification of the northerly wind that promotes the upwelling of nutrient-rich, oxygen-depleted ESSW. The upwelling events promote the bloom of large chain-forming diatoms, mainly *Thalassiosira* spp. and *Chaetoceros* spp. (González et al., 2007). This surplus of autotrophically generated carbon is later grazed by “herbivorous” meso-, nano-, and microzooplankton (Böttjer and Morales, 2007; Vargas et al., 2007), and an important fraction is exported via sedimentation (floculated cells or faecal pellets) to the seabed or advected offshore (González et al., 2007). Vargas et al. (2007) recently reported trophic carbon flow through the primary consumers but, as far as we know, no information exists on the biological response of secondary consumers. Our results demonstrate that the process underlying *S. enflata* maturity in the HCS is much more complex than previously thought, and does not follow a simple association with temperature and prey availability, as previously reported for other areas (Stone, 1966; Sameoto, 1971; Nagasawa, 1984). The possibility that the use of integrated mean values of physical and chemical variables might be responsible for the weak correlation between both the ontogenetic development and feeding patterns of *S. enflata* cannot be ruled out. In fact, the negative correlation between the dissolved oxygen concentrations and the *S. enflata* feeding rate was previously observed in the northern HCS (Giesecke and González, 2004b).
During the two maturity events that could be investigated adequately, a clear correlation was recorded between the number of mature organisms and copepod nauplii abundance. The relationship between these can be explained by an indirect association between both, rather than a direct predator–prey relationship, because nauplii were not found in S. enflata guts. Moreover, nauplii are not expected to contribute substantially to the carbon requirements of S. enflata. We were not able to determine whether S. enflata smaller than 5 mm preyed on nauplii, because the nets used undersampled small chaetognaths.

Increased nauplii abundance, together with the mature S. enflata population previously reported by McLaren (1969), occurred simultaneously with enhanced predation (as FR) on C. chilensis, regardless of its relative abundance (increased selectivity). This, on some occasions, resulted in an increase in the SDR before and during reproduction, similar to the observations made by Kehayias et al. (1996). The selective ingestion of large copepods might account for the surplus energy necessary to cope with the growth and maturation requirements of this species. However, as reported by Reeve (1970), the low capacity of almost all chaetognaths to store lipids (4% of their dry weight) make them “totally dependent” on external lipid availability (Conover and Corner, 1968). Therefore, chaetognaths might need some lipid surplus to fulfil their own vitellogenesis. Reeve (1970) estimated that 41% of the ingested nitrogen is utilized for gamete production, which is equivalent to the ratio incorporated into its own body tissue during early growth. This surplus of energy and nitrogen may be obtained from the ingestion of lipid-bearing organisms that are, in this case, highly available during reproduction of their prey (copepods). If we consider nauplii abundance to be a proxy for copepod reproduction because of the quick egg–nauplii transition (1–2 d at in situ temperatures; Tang et al., 1998), then C. chilensis might account completely or partially for the required amount of lipids necessary to promote oogenesis in S. enflata. The latter suggestion is also supported by Hidalgo and Escribano (2007), who reported high reproductive pulses of C. chilensis during austral spring and summer and intermittent reproduction during winter at the same station (St. 18). The reproduction of some copepods during austral winter was eventually supported by the ingestion of prey other than diatoms, such as micro- and nanoplanckton, which may dominate during these seasons (Böttjer and Morales, 2007; González et al., 2007).

A dependence on external lipids, especially polyunsaturated fatty acids (PUFA), for maturation and reproduction has been extensively reported for crustacean zooplankton in marine and fresh-water environments (reviewed by Brett and Müller-Navarra, 1997; Lee et al., 2006). In the HCS, high abundances of chain-forming diatoms usually promote the egg production rate in calanoid copepods (Peterson et al., 1988), mainly associated with the increase of highly saturated fatty acids in their diet (Vargas et al., 2006). The subsequent accumulation of triacylglycerols and wax esters in oil sacs is characteristic of the copepod genera Calanus, Eucalanus, Paracalanus, Eucalanus, Rhinocalanus, and Pseudocalanus (Lee et al., 2006). The transfer of lipids from primary consumers to higher trophic levels has received less attention, except for a few examples of natural fish and fish larvae (reviewed in Dalsgaard et al., 2003; Varpe et al., 2005). By using fatty acids as trophic markers, St John and Lund (1996) demonstrated that the diatom-based foodweb transfer significantly improves the condition of cod larvae in natural environments, owing to the transport of PUFA through the foodweb.

The only work that deals with the temporal development of total lipid concentrations in chaetognaths (Reeve et al., 1970) was unable to explain the seasonal oscillations by means of temperature, salinity, or food concentrations. Alvarino (1965) observed major discrepancies in reproduction frequency within species in similar environments. Perhaps the limiting of external lipids to fulfil maturity might be one of the main processes controlling the reproductive pulses in chaetognaths and might explain such discrepancies. However, further work is needed to determine the exact mechanisms coupling prey and predator reproduction.

On the other hand, the environment in terms of food quantity and quality, in which the S. enflata offspring develop after large reproductive pulses, might be highly favourable. As shown in Figure 3, the time required for S. enflata to reach maturity (from Stage II to III or IV) took a maximum of 1.5 months (from 0% on 12 November 2002 to 27% Stage III–IV on 27 December 2002), whereas the hatching time after reproduction ranged from 19 to 48 h depending on the temperature (reviewed in Pearre, 1991). Small S. enflata juveniles begin active feeding 8–9 d after hatching (Doncaster, 1902 after Pearre, 1991), when large numbers of copepod nauplii are still available in the environment for the small chaetognaths (<6 mm) to feed on. Potential prey ingested by small S. enflata (<6 mm) should not exceed head width. Therefore, we expect the prey ingested by newly hatched S. enflata to range between a maximum width of 227 and 445 μm for specimens 3 and 6 mm long, respectively, taking

### Table 4. Spearman’s correlations for *Sagitta enflata* feeding activity with biological (prey abundance, chlorophyll *a*), physical (Ekman offshore transport, temperature), and chemical (salinity, dissolved oxygen) variables.

<table>
<thead>
<tr>
<th>Prey abundance (ind. m⁻²)</th>
<th>Chlorophyll <em>a</em> (mg m⁻²)</th>
<th>Ekman S d (m³ s⁻¹)</th>
<th>Temperature (°C)</th>
<th>Salinity</th>
<th>O₂ (ml l⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FCR</td>
<td>-0.07</td>
<td>-0.07</td>
<td>-0.13</td>
<td>0.08</td>
<td>-0.15</td>
</tr>
<tr>
<td>NPC</td>
<td>-0.11</td>
<td>-0.32</td>
<td>-0.31</td>
<td>0.26</td>
<td>-0.17</td>
</tr>
</tbody>
</table>

*p < 0.05.*

![Figure 7](https://example.com/figure7.png)
into account a head-width–body-length ratio of 0.0758 for *S. enflata* (Pearre, 1980). These sizes agree with the sizes of the small calanoid copepod nauplii (116 ± 40 μm) collected during this study (Aparicio, 2006), and *C. chilensis* NI and NII stages (220–330 μm; R. Escribano, pers. comm.).

The presence of a large number of nauplii would, in turn, favour growth of newly hatched *S. enflata* and so diminish their size-dependent vulnerability to predation. However, as shown in Figure 3, the successful establishment of smaller chaetognaths did not seem to be related to the reproduction intensity but to the temporal extension of the reproductive event that coincides with the occurrence of large numbers of nauplii. After the strong 2002/2003 spawning event, the abundance of recently hatched *S. enflata* was low in subsequent months, possibly associated with the recruitment failure that was likely caused by the poor availability of food for the small juveniles. The near absence of smaller *S. enflata* after the 2002/2003 reproductive pulse seems not to be a consequence of the limited sampling procedure (monthly). This was determined because, not only were small sizes (<6 mm) scarce, but large sizes (7–9 mm) were also scarce in the following 2 months (R. Giesecke, unpublished). During the two later reproductive events (2003/2004, 2004/2005), in which an extended breeding period was achieved and a continuous abundance of nauplii available, a significant proportion of the entire population was made up of newly hatched chaetognaths. We cannot, however, dismiss the possibility that the low abundance of small chaetognaths in the following months after the first peak in reproduction might be a consequence of advection processes of small organisms transported offshore during the prevailing upwelling conditions in austral spring and summer.

Based on the results of this study, we propose a conceptual model (Figure 8) in which the onset of favourable food conditions for oogenesis and reproduction in copepods triggers a chain reaction that starts with the selective predation of *S. enflata* on large lipid-bearing copepods (such as *C. chilensis*) while favouring lipid storage in *S. enflata* Stages I and II for reaching maturity (Stages III and IV). Once mature organisms have reproduced and the hatched offspring start to feed, the considerable number of copepod nauplii remaining in the environment as a result of the copepod reproduction that triggered chaetognath maturity create favourable food conditions for newly hatched chaetognaths.

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**References**


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![Figure 8](https://example.com/figure8.png)

**Figure 8.** Conceptual scheme of the associations between copepod maturity and the feeding activity and oogenesis of *Sagitta enflata* and the possible association between their recently hatched offspring. Favourable food conditions for copepod reproduction are linked with selective predation of *S. enflata* upon large oil-sac-bearing copepods (*Calanus chilensis*). This process may allow the incorporation of lipids by *S. enflata*, which are later used for their own oogenesis. The offspring produced during these reproductive pulses are released into an environment with large numbers of potential prey, which would favour their development.


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